

# Assessing changes in biomass, productivity, and C and N stores following *Juniperus virginiana* forest expansion into tallgrass prairie

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**Abstract:** An increase in woody plant abundance in regions historically dominated by grasses is a recent land cover change in grasslands worldwide. In tallgrass prairies of North America, this increase in woody plant cover includes the development of dense stands of eastern redcedar (*Juniperus virginiana* L.). To evaluate the consequences of this ongoing land cover change for ecosystem functioning, we developed allometric equations, using data from Kansas and Oklahoma, to estimate aboveground biomass and productivity in closed-canopy redcedar stands. We then applied these equations to three closed-canopy redcedar stands, 35–80 years old, which developed on sites formerly dominated by tallgrass prairie in eastern Kansas. Aboveground plant biomass for these redcedar-dominated sites ranged from 114 100 kg/ha for the youngest stand to 210 700 kg/ha for the oldest. Annual aboveground net primary productivity (ANPP) ranged from 7250 to 10 440 kg·ha<sup>-1</sup>·year<sup>-1</sup> for the oldest and younger redcedar stands, respectively. Estimates of ANPP in comparable tallgrass prairie sites in this region average 3690 kg·ha<sup>-1</sup>·year<sup>-1</sup> indicating a large increase in C uptake and aboveground storage as a result of the change from prairie to redcedar forests. Therefore, the widespread occurrence of redcedars across the woodland–prairie ecotone suggests that this land-cover change may have important consequences for regional net C storage.

**Résumé :** L'augmentation de l'abondance des plantes ligneuses dans des régions historiquement dominées par les graminées est un changement récent de type de couvert des prairies à l'échelle mondiale. Dans les prairies à herbes hautes de l'Amérique du Nord, cette augmentation du couvert des plantes ligneuses inclut le développement de peuplements denses de genévrier de Virginie (*Juniperus virginiana* L.). De façon à évaluer les conséquences de ce changement progressif de type de couvert pour le fonctionnement de l'écosystème, nous avons développé des équations allométriques à partir de données provenant du Kansas et de l'Oklahoma pour estimer la biomasse épigée et la productivité de ces peuplements à couvert fermé de genévrier. Nous avons ensuite appliqué ces équations à trois peuplements fermés de genévrier, âgés entre 35 et 80 ans et qui se sont développés dans des sites anciennement dominés par la prairie à herbes hautes dans l'est du Kansas. La biomasse aérienne de ces sites dominés par le genévrier variait de 114 100 kg/ha pour le peuplement le plus jeune à 210 700 kg/ha pour le plus vieux. La productivité primaire nette annuelle de la biomasse aérienne (PPNA) oscillait entre 7250 et 10 440 kg·ha<sup>-1</sup>·an<sup>-1</sup> respectivement pour le plus vieux et le plus jeune peuplement. Les estimés de la PPNA dans des sites de prairie à herbes comparables atteignent en moyenne 3690 kg·ha<sup>-1</sup>·an<sup>-1</sup>, ce qui indique une forte augmentation de la fixation du carbone et de son stockage aérien par la conversion des prairies en forêts de genévrier. Par conséquent, la présence abondante de genévriers dans l'écotone prairie-forêt semble indiquer que ce changement de type de couvert peut avoir des conséquences importantes pour le stockage régional net de carbone.

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## Introduction

In the past few decades, woody plant growth has increased in grasslands and savannas worldwide (Archer 1995;

Archer et al. 1995). These recent increases in woody plant cover in regions historically dominated by grasses have been attributed to a variety of factors including changes in climate, changes in land use (fire frequency, grazing patterns), elevated N inputs, and increased atmospheric CO<sub>2</sub> (Owensby et al. 1973; Archer 1993; Polley et al. 1994; Scholes and Archer 1997). Land-cover change of this magnitude is likely to affect key ecosystem processes in grasslands, which in some regions may significantly alter carbon cycling and feedbacks to climate change. One of the woody plant species that has increased in abundance in the tallgrass prairie region of North America is eastern redcedar (*Juniperus virginiana* L., hereafter called redcedar). Redcedar is a widely distributed tree species, found in every state east of 100°W (Fowells 1965). In the last century, increased abundance and cover of redcedar within this range has been documented in mid-Atlantic, southeastern, and most notably, in midwestern states historically dominated by tallgrass prairie (Blan 1970;

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Owensby et al. 1973; Bragg and Hulbert 1976; Holthuijzen and Sharik 1985; Blewett 1986; Holthuijzen et al. 1987; Schmidt and Leatherberry 1995). Throughout much of its range, redcedar is noted for being a pioneer species capable of invading abandoned agricultural fields (Fowells 1965; Holthuijzen et al. 1987) and grasslands that are not burned (Ormsbee et al. 1976), suggesting that recent changes in land uses underlie the expansion of redcedar in regions which were historically grazed and subject to frequent fires. For example, Owensby et al. (1973) noted that, only when fire is excluded in tallgrass prairie, can redcedar compete with native grasses and develop dense, nearly monospecific, closed-canopy stands.

In the midwestern United States, the extensive expansion of redcedar stands into a region historically occupied by  $C_4$  grass-dominated tallgrass prairie has potentially important implications for local and regional biodiversity and biogeochemistry. For example, the development of dense stands of redcedar is associated with a reduction in the biomass and diversity of understory plants (Hoch and Briggs 1999). In addition, the shift from grasses and herbaceous plants to coniferous tree species is likely to change plant productivity, standing plant biomass, and the relative allocation and storage of carbon in above- and below-ground components. Tallgrass prairie is one of the most productive grassland types in North America, with a high rate of aboveground plant productivity (Knapp et al. 1998), a large proportion of plant biomass occurring belowground, and an associated large accumulation of soil organic carbon (Rice et al. 1998). In areas of prairie that have been overtaken by forests, there is likely to be a substantial increase in aboveground biomass and associated C storage (Olson et al. 1985), although this increase aboveground may be offset by reductions in the belowground compartments (Schlesinger 1977). Although changes in ecosystem properties and processes have been observed with woody plant expansion in other grasslands (Archer et al. 2001), the net effect of these potential changes in C allocation is unknown for redcedar stands that have recently replaced areas of tallgrass prairie.

Currently, closed-canopy redcedar forests occupy as much as 1.4% of northeastern Kansas counties (Hoch and Briggs 1999) with the areal extent of these closed-canopy stands increasing by 120% from 1983 to 1997. Perhaps of greater concern is the amount of land currently covered with less dense stands of redcedar. In 1997, 10.4% of a 7180-ha study area in the northern Flint Hills was classified as open-canopy (40–80% cover) redcedar stands, an increase of 80% over the previous 14 years (G. Hoch and J. Briggs, unpublished data). If these open-canopy stands continue to develop into dense closed-canopy stands of redcedar, we can expect considerable shifts in the community composition and perhaps biogeochemistry of this region.

The objective of this project was to assess the changes in plant productivity and aboveground plant biomass associated with eastern redcedar forest expansion into areas formerly dominated by tallgrass prairie. To do this, we first developed regionally appropriate allometric biomass regression equations for the nondestructive estimation of redcedar biomass in eastern Kansas. We also quantified the C and N content of selected biomass components. Then, we applied these equations, along with measurements of leaf litter production, to

selected local stands of mature closed-canopy redcedars to estimate aboveground biomass, standing stocks of C and N, and annual aboveground net primary productivity. These results were then compared with similar published data from comparable local tallgrass prairie sites, thereby allowing us to contrast ecosystem characteristics for the endpoints of the ongoing redcedar expansion in tallgrass prairie.

## Methods

### Study areas

For the development of the allometric equations, we destructively sampled trees from two sites located near Manhattan, Kan., in the Flint Hills region of northeastern Kansas. The local climate is characterized as temperate midcontinental with a mean annual temperature of 13°C and mean annual precipitation of 835 mm, of which about 75% occurs in the growing season. In general, soils of this area are characterized as cherty silty clay loams with variable depth to bedrock. Six sample trees ranging in size from 13.7 to 32.8 cm diameter at breast height (DBH) were harvested from closed-canopy stands of redcedar at two locations. One site (39°10'N, 96°39'W) was a former upland pasture in which redcedars, approximately 35 years old, formed a monospecific stand that was highly uniform and dense. Trees from the second site (39°14'N, 96°30'W), located in gallery forest surrounded by grassland, were nearly 70 years old (G. Hoch, personal communication). The forest stand at this site was much less dense and exhibited greater heterogeneity in species composition and topography compared with the first site. The data from the Kansas sites were compared with, and then combined with, similar data extracted from a previous study in north-central Oklahoma (Lykins 1995) for a total of 12 trees representing a range of sizes and diameters (13.3–37.3 cm DBH) and a wide range of soil, site, and climatic variables, providing regional applicability to the allometric equations. Climate in the Oklahoma study counties had a range of mean annual temperature of 14.4–15.8°C and mean annual precipitation of 605–889 mm. Soils were predominantly loamy sands or sandy loams (Lykins 1995).

The allometric equations developed above were then used to estimate aboveground biomass and productivity of closed-canopy redcedar stands at three separate study sites in northeastern Kansas (Table 1). The mean age of the redcedar trees at these stands ranged from approximately 35 to 80 years old, based on tree increment cores and historical aerial photography (G. Hoch and J. Briggs, unpublished data). Two stands were younger (approximately 35–40 years old), with a denser and more uniform tree distribution than the oldest stand (Table 1). In all three closed-canopy redcedar stands, understory vegetation was very sparse and was not included in biomass and productivity estimates.

### Development of allometric equations

Processing of redcedar trees sampled in Kansas for the development of the allometric equations was patterned after methods described by Lykins (1995) for processing trees sampled in Oklahoma. After felling at ground level, trees were cut into components including live branches, dead branches, and manageable 1.5- to 2-m sections of the bole. Live branches, dead branches, and sections of bole were weighed (fresh mass) on an electronic balance. Disks (3–6 cm thick), cut from the bottom of each section of bole and subsamples of 5–10 representative branches (both dead and alive) were returned to the laboratory and oven-dried to determine moisture content before further processing. In the laboratory, live branches were cut and divided into segments based on three diameter size classes: >2.5 cm, 0.6–2.5 cm, and <0.6 cm including foliage. Moisture contents and dry masses of the samples were calculated by drying components at 60°C to a constant mass (3–

**Table 1.** Description of sites used for application of allometric regression equations and the resulting estimates of aboveground biomass and productivity.

Site No.	Location	Latitude (N)	Longitude (W)	Topographic position	Age (years)	Density (trees/ha)	Total aboveground		Annual WGI (kg·ha <sup>-1</sup> ·year <sup>-1</sup> )*	Litter fall production (kg·ha <sup>-1</sup> ·year <sup>-1</sup> )	ANPP (kg·ha <sup>-1</sup> ·year <sup>-1</sup> )
							biomass (kg/ha)	Biomass C (kg/ha)			
1	Scenic Drive	39°10'	96°39'	Upland slope	35	1733	114 120	61 563	4606	5190	9 796
2	Tuttle Creek	39°17'	96°34'	Upland slope	80	860	210 952	106 192	2637	4610	7 247
3	Dam Randolph	39°27'	96°45'	Upland	40	1900	120 739	65 451	5232	5210	10 442

\*WGI, woody growth increment (annual change in biomass).

5 days). Bole disks were divided into bark, sapwood, and heartwood components by chisel and weighed.

Three subsamples were taken randomly from each component sample from each tree (bole disk components, live branch components, and dead branches) and analyzed for carbon and nitrogen content. Samples were homogenized by grinding and analyzed by dry combustion and gas chromatography for percent C and N on a Carlo Erba NA 1500 analyzer (Carlo Erba, Milano, Italy). Total tree biomass C and N was determined by summing the products of mean nutrient content values and the associated weight of the tree components.

Allometric equations relating dry aboveground biomass (kg) to DBH (cm) were determined for each tree component as well as for total tree biomass, biomass C, and biomass N. Equations were developed as log-log functions as described by Whittaker and Marks (1975) using SAS PROC REG (SAS Institute Inc. 1996).

### Estimating aboveground biomass of redcedar stands

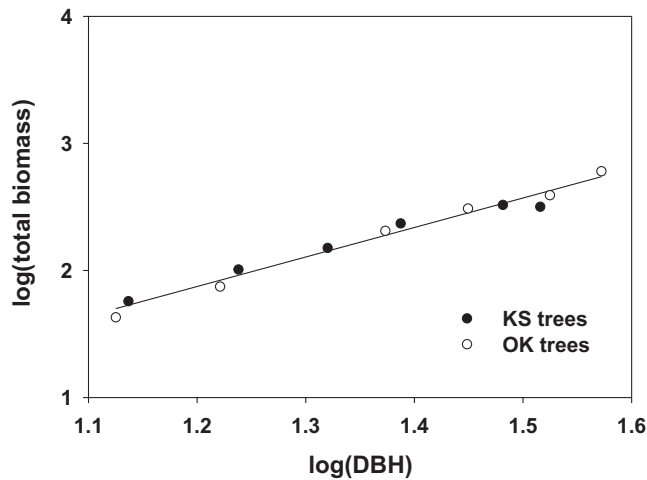
To estimate aboveground plant biomass in the redcedar stands at each of the three study sites, three 0.02-ha circular (7.98 m radius) sample plots per site were established. These plots were evenly spaced along a 200-m transect bisecting the interior of each stand. Several relatively small plots were used, instead of one large plot, because of the high density of trees (20–40 trees per 0.02-ha plot) and to more effectively account for any stand heterogeneity. Each tree in each plot was measured for DBH (cm), and the DBH of each tree was used in the allometric equations to calculate individual tree biomass. The masses of all individual trees in a plot were then summed to calculate redcedar biomass for each plot, and the plot values were averaged to estimate stand-level redcedar biomass on an areal basis at each of the three sites. A similar approach was used to estimate quantities of C and N associated with the aboveground tree biomass at each site.

### Estimating aboveground productivity of redcedar stands

Data from the same three stands used to estimate aboveground redcedar biomass were used to estimate annual aboveground net productivity of the redcedars. Annual aboveground net primary productivity (ANPP) was estimated using the equation  $ANPP = \Delta B + L$ , where  $\Delta B$  is the annual increase in aboveground tree biomass and  $L$  is annual litter fall (modified from Newbould 1967). Annual biomass changes were estimated based on annual changes in DBH, calculated from tree increment cores taken at breast height from 12–20 trees along the same 200-m transects (M. Pline and G. Hoch, unpublished data). For each tree cored, an average incremental growth (in diameter) for the previous 5 years was determined, taking care to account for false rings (Kuo and McGinnes 1973). The average annual incremental increase in DBH was then subtracted from the current diameter to estimate the average previous year's diameter. An average change in diameter over 5 years was used to account for annual climatic variation (i.e., dry vs. wet years). Both the current diameter and the mean previous year's diameter were used in the allometric equations to estimate total aboveground annual productivity referred to as woody growth increment (WGI). We refer to the annual change in total aboveground tree biomass as the woody growth increment, because change in foliar biomass is a minor component of ANPP (data not shown). Woody growth increment and current DBH was determined for each sampled tree, then used to develop regression equations of WGI versus DBH that could be applied to all of the trees in the plots sampled for biomass. Equations were calculated for each individual study site as well as for the three sites pooled. Resulting values represented the annual  $\Delta B$  in each stand.

Litter fall collectors were used to determine litter production in the same three stands over a period of 2 years. Twenty square col-

**Fig. 1.** Twelve trees were harvested from closed canopy redcedar forests in north-central Oklahoma (OK) and northeastern Kansas (KS) to develop allometric equations for total redcedar biomass (kg) versus DBH (cm). Equations were established as log–log functions.



**Table 2.** Parameters, coefficient of determination, and significance of the allometric equation relating biomass of whole trees ( $n = 12$ ) and specific components (kg) to DBH (cm).

Biomass component	A	B	$r^2$	p
Total redcedar tree biomass	-0.912	2.322	0.978	0.0001
Live branches				
Foliage	-1.308	2.002	0.893	0.0001
0.64–2.54 cm	-0.968	1.592	0.763	0.0002
>2.54 cm	-3.716	3.632	0.840	0.0001
Total	-1.34	2.301	0.885	0.0001
Total dead branches	-1.715	2.123	0.660	0.0013
Bolewood				
Heartwood	-1.866	2.624	0.941	0.0001
Sapwood	-1.081	1.949	0.920	0.0001
Bark	-2.432	2.347	0.849	0.0001
Total	-1.207	2.340	0.948	0.0001

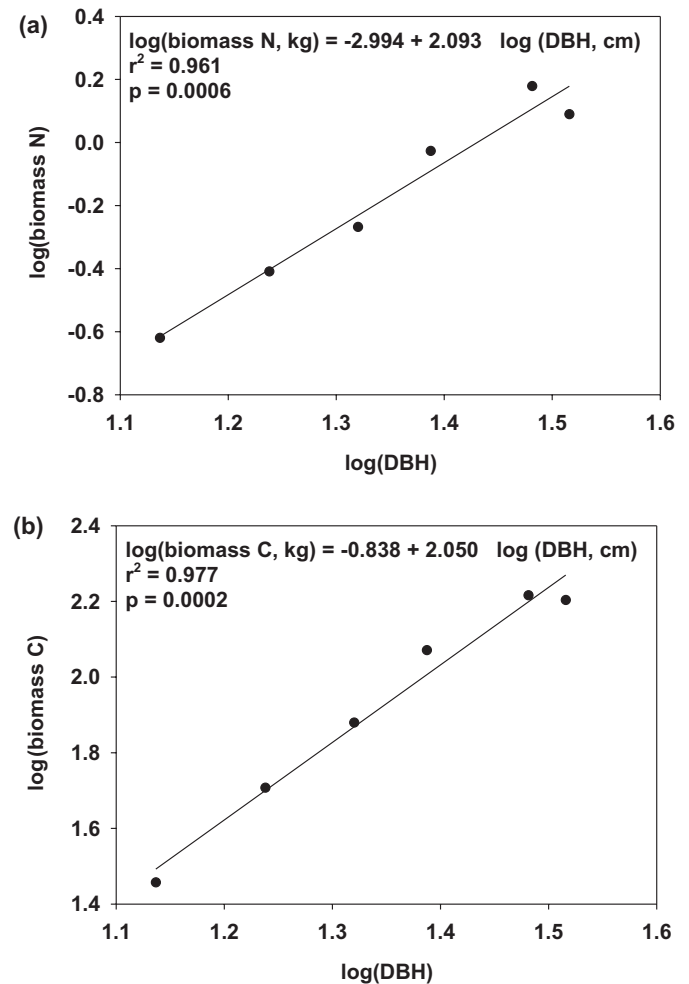
**Note:** The allometric equation is as follows:  $\log(\text{biomass}) = A + B \log(\text{DBH})$ .

lectors ( $0.25 \text{ m}^2$ ) were placed along a 200-m transect at each site. Collections were made monthly from October 1997 through October 1999. Litter was oven-dried at  $60^\circ\text{C}$  for 48 h and weighed. The ANPP was then calculated as above.

## Results

The DBH of eastern redcedars was a good predictor of aboveground tree biomass, and trees from both Kansas and Oklahoma fit the same allometric equations relating biomass to DBH (Fig. 1). Coefficients of determination ( $r^2$ ) for the allometric equations relating DBH to biomass ranged from 0.660 for dry biomass of dead branches to 0.978 for whole tree biomass (Table 2). All regressions were significant ( $p < 0.01$ ). In most cases, equations for the total biomass of major components (i.e., bolewood or live branches) exhibited greater  $r^2$  values than those of the individual subcomponents (i.e., specific size classes of branches). Regressions of DBH versus biomass C and N were also significant and produced

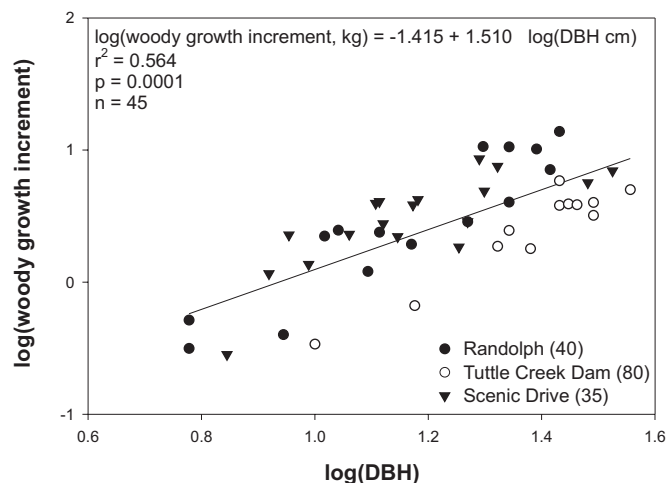
**Fig. 2.** Regressions of biomass nutrient versus DBH for six redcedar trees harvested in northeastern Kansas were developed to estimate N and C content of closed canopy stands. Equations were determined for biomass N (a) and biomass C (b).



high regression coefficients (Fig. 2). Regressions relating DBH to the woody growth increment of trees at individual sites were all significant, but produced lower  $r^2$  values as a whole, ranging from 0.631 for the younger study site to 0.905 for the oldest. The woody growth increment regression using data pooled from all sites (Fig. 3) exhibited the lowest  $r^2$  ( $r^2 = 0.56$ ) but was still significant ( $p = 0.0001$ ).

The C and N content of specific redcedar components varied. Although carbon concentrations of all tree components were similar ( $\sim 50\%$  C), N concentrations varied more than fivefold for different components (Table 3). As expected, heartwood had the lowest nitrogen content (0.19%) and foliage had the highest N content (1.09%). As a result of these differences in N content, the relative contributions of individual tree components to standing stocks of plant biomass C and N varied considerably. For a range of tree DBHs (15–30 cm), bolewood (heartwood + sapwood + bark) accounted for an average of 56% of total tree biomass and standing C but only 34% of the total standing stocks of tree N. In contrast, foliage averaged only 15% of tree biomass and C stocks but accounted for the largest single pool (44%) of total tree biomass N.

**Fig. 3.** Regression of woody growth increment versus DBH to estimate annual change in aboveground biomass (woody growth increment) for redcedar trees in three stands of varying age in northeastern Kansas.



Estimates of aboveground biomass at our three study sites ranged from approximately 114 000 to 211 000 kg/ha (Table 1). Of the three study sites, two were relatively close in age (approximately 35 and 40 years) and half the age of the other site (80 years). The oldest site had much lower tree density and twice the biomass of the younger sites (Table 1). Stand-level estimates of aboveground biomass C and N in redcedars exhibited patterns similar to those for total plant biomass. Calculated standing stocks of biomass C of the stands were between 50 and 55% of the total stand biomass, which was slightly more than the measured average carbon concentrations of individual tree components (Table 3). Standing stocks of biomass N were approximately 0.4% of total biomass of the stands. When the woody growth increment was summed with the litter fall data from each site, estimates of total annual aboveground net primary production ranged from 7247 kg·ha<sup>-1</sup>·year<sup>-1</sup> for the oldest site to 10 442 kg·ha<sup>-1</sup>·year<sup>-1</sup> for one of the younger sites (Table 1).

## Discussion

The fit of biomass and DBH data from trees at both the Kansas and Oklahoma sites to a single allometric equation, despite differences in climate and soils, suggests that our allometric equations may be applicable to a relatively large geographic area of the eastern Great Plains. In consideration of the broad ecological range of sites used, the relatively high coefficient of determination for the allometric equations developed to estimate total tree biomass ( $r^2 = 0.98$ ) is somewhat surprising (Fig. 1). For example, the climate at the Oklahoma sites was slightly warmer and drier compared with the Kansas sites. Additionally, there were major differences in soil properties. Therefore, the similarity of the allometric relationships for trees from Kansas and Oklahoma and the high regression coefficients for these equations suggests particular uniformity of the redcedar species, at least within the eastern Great Plains region. This suggests that these allometric equations may be generally applied throughout the Flint Hills and possibly a wider geographic range, facilitating regional studies of redcedar forest expansion. However, we also note that trees from Oklahoma and

**Table 3.** Carbon and nitrogen concentrations (% dry mass) of eastern redcedar tree components ( $n = 93$ ).

Redcedar component	% C	% N
Live branches		
Foliage	50.89	1.09
0.64–2.54 cm	49.02	0.34
>2.54 cm	49.57	0.25
Total dead branches	49.66	0.27
Bolewood		
Heartwood	51.54	0.19
Sapwood	49.96	0.22
Bark	47.91	0.65

Kansas exhibited different patterns of age–size relationships. Trees of a particular DBH harvested in Oklahoma were nearly twice the age of similarly sized trees in Kansas (Norris 2000), perhaps because of greater drought stress and poorer soils at the Oklahoma sites.

In contrast to the generality of a single allometric equation for biomass, the relationships between DBH and woody growth increment exhibited the best fits when calculated for the individual sites. Using pooled data from all sites, the equation underestimated woody growth increment of younger stands and overestimated that of older sites (Fig. 3). This indicates that there is an age-related decline of productivity in redcedar forests as has been found elsewhere for other forest types (Ryan et al. 1997). Therefore, developing site-specific allometric equations of woody growth increment using increment cores and the allometric biomass equations in Table 2, or perhaps, a multivariate approach accounting for stand age would be preferred for estimating stand-level productivity. Furthermore, considering the age–size relationship of the Oklahoma trees compared with Kansas trees, woody growth increment regression equations from one region will not necessarily be suitable to another.

Annual litter fall estimates were variable among the study sites, depending on stand density and age (Table 1). The oldest site had slightly lower mean litter fall rates (4610 kg·ha<sup>-1</sup>·year<sup>-1</sup>) compared with the two younger sites (5200 kg·ha<sup>-1</sup>·year<sup>-1</sup>). Because litter fall exhibited the same declining relationship with respect to age as woody growth increment, it further contributes to the decline in ANPP over time at these redcedar sites. We are aware that using litter fall rates to estimate foliar productivity may result in underestimates, because of losses of leaf mass by herbivory and early rapid decay. However, given the low rates of herbivory and slow decay rates characteristic of redcedar (Norris et al. 2001), it is doubtful that these losses were significant in this study.

Rates of annual aboveground production of the redcedar stands were substantially greater than the grasslands that these forests are replacing. Our estimates of ANPP in the redcedar stands (7247–10442 kg·ha<sup>-1</sup>·year<sup>-1</sup>) were nearly two to three times greater than the long-term average annual productivity of nearby annually burned prairie in a similar upland topographic position (20-year mean ANPP 3690 kg·ha<sup>-1</sup>·year<sup>-1</sup>; range 1780–5700 kg·ha<sup>-1</sup>·year<sup>-1</sup>; Knapp et al. 1998). Although upland prairie sites provide the most appropriate comparisons, since redcedar stands tend to become established primarily on upland sites, lowland prairie

sites are generally more productive because of increased water availability. However, even in these lowland sites, ANPP of the native prairie averages only  $5275 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$  (range  $2790\text{--}7850 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ ) (Knapp et al. 1998), which is still much less than our estimates for redcedar forests. The substantial increase in annual aboveground productivity associated with conversion of prairie to redcedar-dominated stands could lead to a significant increase in regional carbon storage, especially in consideration of the extensive amount of tallgrass prairie recently encroached upon by redcedar stands.

The redcedar stands examined in this study store much more C and N aboveground in plant biomass than do the tallgrass prairies they have replaced. Total aboveground biomass at the three redcedar study sites ranged from approximately 114 000 to 211 000 kg/ha (Table 1), while 10-year means of total aboveground plant biomass (live plants + standing dead) in native prairie range from 3890 kg/ha (burned upland prairie) to 9230 kg/ha (Abrams et al. 1986). Associated with the greater aboveground biomass of the redcedar stands are greater stores of C and N. Using an average C content of 44.5% for herbaceous biomass in tallgrass prairie (J. Blair, unpublished data), storage of C in aboveground plant biomass in tallgrass prairie ranges from about 1730 to 4110 kg C/ha, while our estimates of aboveground biomass C in the redcedar stands ranges from 61 563 to 106 192 kg C/ha. Native tallgrass prairies in this region store about 20–130 kg N/ha in aboveground plant biomass + standing dead vegetation (Blair et al. 1998), compared with 487–849 kg N/ha in the redcedar stands (Table 1). Thus, the conversion of tallgrass prairie to redcedar-dominated stands is accompanied by substantial increases in C and N storage in aboveground biomass. Allometric equations for specific tree components indicate patterns of C and N allocation within the redcedar tree. For instance, bolewood contains the greatest portion of the tree's biomass and C (56%) but has a much small proportion of tree N, which is mostly stored in foliage.

An important caveat concerning our interpretations of the impact of changes in aboveground production on net C storage in redcedar stands concerns patterns of belowground productivity and C storage. Although results of an ongoing study at the same redcedar stands used in this study indicate no reductions in total soil C with encroachment of redcedar stands into native grassland sites (D. Smith and L. Johnson, unpublished data), there is greater uncertainty surrounding root dynamics because belowground productivity in grasslands is believed to be a significant portion of total net primary productivity (NPP) (Rice et al. 1998). At Konza Prairie, Seastedt and Ramundo (1990) estimated root biomass (excluding rhizomes) to a depth of 30 cm to be  $8590\text{--}10\,860 \text{ kg/ha}$ , which is two to four times the aboveground component. Although our study did not quantify belowground biomass or productivity for the redcedar stands, we can begin to address this issue with some basic assumptions. Our biomass and productivity calculations were revisited using the assumptions that total root biomass (including fine roots) in upland redcedar forests is 25% of the aboveground portion (Cairns et al. 1997) and changes proportionally with aboveground woody growth increment. This estimate of root biomass was derived from studies of other temperate conifer

forests on fine soils. Assuming a root/shoot ratio of 0.25, estimates of belowground biomass in our study sites range from approximately  $28\,530 \text{ kg/ha}$  for the youngest site to  $52\,740 \text{ kg/ha}$  for the oldest, resulting in estimates of total biomass ranging from  $142\,650$  to  $263\,690 \text{ kg/ha}$ , which is more than an order of magnitude greater than total prairie peak biomass ( $14\,550 \text{ kg/ha}$ ; Seastedt and Ramundo 1990; Knapp et al. 1998).

If our woody growth increment equations are recalculated to include roots in the same manner as above, we obtain new growth increment values (above- and below-ground) of approximately  $3300$ ,  $5750$ , and  $6530 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$  for the three sites (ages 80, 35, and 40 years, respectively). When summed with litter fall, we arrive at a range of NPP of  $7910\text{--}11\,740 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ . For comparison, belowground production in an annually burned upland grassland in this area was estimated at  $4500 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$  by the root-ingrowth bag method (Johnson and Matchett 2001). Therefore, total NPP in annually burned upland grasslands is approximately  $8190 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ , which is in the lower portion of the range for total redcedar production and well below our estimates for the more productive, younger stands. We must emphasize that these belowground productivity estimates are first approximations (i.e., based on assumed root/shoot ratios and ignoring fine root turnover) and are only used for this preliminary comparison. Furthermore, there are complex relationships with forest age and grassland environmental factors, especially burning and grazing regime and topographic position. However, even considering the much higher rates of belowground NPP in prairie, the most productive of the redcedar study sites was  $3550 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$  greater than the prairie.

Our estimates of total productivity for these redcedar stands are below the mean productivity for temperate forests provided by Whittaker (1975) (mean  $12\,500 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ ; range  $6000\text{--}25\,000$ ). Lower ranges of productivity for redcedar forests are reasonable, and perhaps expected, given their geographical location in the ecotone between eastern temperate deciduous forest and grassland where decreased precipitation and historical burning regime limit forest establishment.

Frequent fires were historically critical for maintaining the tallgrass prairie landscape of the eastern Great Plains, and in the absence of a regular burning regime, grass production declines (Knapp and Seastedt 1986) and a shift in species composition to a greater abundance of woody vegetation, including eastern redcedar, can occur (Gibson and Hulbert 1987; Knight et al. 1994; Briggs and Knapp 1995). This study suggests that in areas where redcedar has become established and formed closed-canopy stands local C uptake and accumulation in plant biomass increases, at least temporarily. However, the effects of redcedar establishment on net ecosystem C exchange (including soil and detrital C) is not yet known, and additional data are needed for a more thorough consideration of belowground C dynamics (i.e., fine root turnover, detrital decomposition, and soil respiration). Nonetheless, these forests represent a shift in productivity and C storage from belowground to aboveground compared with the prairie. When coupled with the land area of grassland that is being replaced by redcedar (Schmidt and Leatherberry 1995; Hoch and Briggs 1999), increased C

storage as suggested here may be impacting other biogeochemical cycles (N and H<sub>2</sub>O) at larger spatial scales.

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